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Evolutionary ecology of the North Atlantic Talitridae (Crustacea, Amphipoda): A review

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Abstract

Four primary estuarine/marine ecotopes recognized in the North Atlantic continental littoral and continental terrestrial margins give rise to the following ecotypes: wrack generalists (=beach-hoppers), psammophilic talitrids (=sandburrowing-hoppers), palustral talitrids (=salt marsh-hoppers), and xylophagous talitrids (=driftwood hoppers). On the European continent, there are freshwater riverine and lacustrine talitrids. In addition, there are a few terrestrial ecotypes in the Northeast Atlantic Islands: rainforest leaflitter talitrids and one troglobiont (=cave-hopper). Wrack generalist species are phenotypically plastic and can live in one or more secondary ecotopes. It is hypothesized herein that switching on/off appropriate genes by cellular mechanisms (epigenesis) occurs during the microevolution of Talitridae. The generalist/specialist continuum concept supports our understanding of both the ecology and microevolution of talitrids. Microevolutionary characteristics of wrack generalists are that they exhibit the most phenotypic variability and occurrences of epigenesis, have the most extensive zoogeographic range, and have the lowest speciation potential and endemism rate. Examples where epigenesis may be part of the microevolutionary process include low/high salinity and hypogean/epigean combined switches giving rise to sibling (sister) species pairs. Current views of the phylogeny of the Talitridae based on either morphological characters used in taxonomy or molecular genetic methods are still under development. Molecular genetic methods show promise of providing a scientifically reproducible phylogeny and temporal history of talitrids (macroevolution), but insufficient coverage of genera within talitrids and of related groups is available to do so yet.

Key Words

Generalist/specialist continuum, micro-/macro-evolution, primary and secondary talitrid ecotypes, sibling species pairs, Talitridae

Introduction

The Talitridae (talitrids) are a family within the Amphipoda, which in 2018 consisted of 80 genera and 512 species worldwide (Tykarska et al. 2019), with new genera and species being added annually. Many of the new talitrid species described do not contain adequate ecological descriptions of the type locality (Lowry and Myers 2019).

Talitrids are found in many ecotopes (=ecological habitats or niches) from marine and estuarine to freshwater to terrestrial (Hurley 1968; Friend and Richardson 1986; Wildish 1988). A current summary of the established ecotopes occupied by talitrids on the shores of the Atlantic Ocean is shown in Table 1. This is a preliminary list because only a few talitrids, mostly in the temperate North Atlantic, have been adequately studied from an ecological perspective. As further ecological studies, notably on southern hemisphere terrestrial species, are completed, further ecotopes will be added to a world list expanded from Table 1.

Evolutionary studies of talitrids include changes that occur at very different temporal and spatial scales. Both scales are continuous, making it difficult to characterize the particular evolutionary changes of concern. Here I consider microevolution to result from a limited number of environmental factors and genetic or epigenetic changes in one or a few species. By contrast, macroevolution involves all species within the family Talitridae from

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their origin millions of years ago from an amphipod stem group to their radiation to most parts of the world today.

This presentation is an update and expansion of a review dealing only with xylophagous talitrids (Wildish 2017). The expansion includes new ecological discoveries and microevolutionary findings concerning Talitridae in all ecotopes of the North Atlantic coastal region. This includes the Gulf of Mexico and the Mediterranean Sea, Atlantic islands, and the terrestrial ecotopes of the Northeast Atlantic islands (Azores, Madeira, and Canaries Archipelagos).

Primary and secondary ecotopes

In ecology, we require an accurate descriptive nomenclature for each talitrid ecotype (a talitrid species occupying and adapted to a particular ecotope) recognized so that it is possible to refer each species to an ecotope within a given ecosystem (Table 1). For this reason, the term "semi-terrestrial" as occasionally used in the literature for marine intertidal talitrids (e.g., Hupalo and Grabowski 2018) is inadmissible in ecology because there is no ecosystem to which it is referable. Thus, wrack generalists (as here defined) are never "semi-terrestrial" and are more accurately described in an ecological sense as 'amphibious' because they live in both damp air in the intertidal zone and sometimes in seawater (at high tide and occasionally during passive seawater dispersal). Table 1 considers only primary ecotypes and represents a work in progress, as it is expected that many more ecotopes and ecotypes remain to be discovered and described from other parts of the world. Primary ecotopes are ones in which a given species is usually found and to which it has evolved characteristic adaptations. It is contrasted with one or more secondary ecotopes, in each of which the same species is less commonly found and lacks some of the characteristic adaptations of the primary ecotype (Wildish and Robinson 2016a).

The most studied ocean system concerning talitrid ecology is the coastal North Atlantic, inclusive of the Gulf of Mexico and the Mediterranean Sea, with a species and ecotype list given by Wildish and Chang (2017). This list is summarized in Table 2. It does not include the northeast Atlantic Island talitrids; they are dealt with separately below. There is disagreement regarding the zoogeography of *Orchestia gammarellus* (Pallas, 1766) in the northwest Atlantic (Canada and Iceland), with Myers and Lowry (2020) suggesting that it is a new species despite the molecular genetic evidence of Henzler and Ingolfsson (2008) that it is the same species on both sides of the North Atlantic. Wildish and McDonald (2023) have proposed a natural, passive dispersal hypothesis to account for the presence of *O. gammarellus* in post-glacial Iceland and Canada. The other amphi-Atlantic species of Table 2 are *Platorchestia exter* Myers & Lowry, 2023, and *P. oliveirae* Myers & Lowry, 2023. These two species are the dominant wrack generalists of the coastal northwest Atlantic with a zoogeographic range from Brazil to Newfoundland. *Platorchestia exter* occupies the northerly part and *P. oliveirae* the more southerly part of this range, with the separation occurring somewhere in, or north of, Florida. It has been hypothesized (Wildish and Chang 2017) that both species reached the northeast Atlantic coast recently either by natural, passive rafting carried by Gulf Stream currents or by synanthropy. Preliminary molecular genetic evidence that the European *Platorchestia* are the same species as those from North America is available (Radulovici 2012; Hupalo and Grabowski 2018).

It was discovered by field observations in 2015 that *P. exter* could occupy a secondary ecotope: stranded driftwood (Wildish and Robinson 2016a) when specimens were found occupying this habitat in a driftwood depository in the Bay of Fundy. This study also confirmed that *P. exter* could be cultured solely on driftwood as food for at least six months. Driftwood acclimation, which involves ingesting rotting driftwood, resulted in reduced growth and shorter adult total body lengths (Table 3).

Table 1. Primary talitrid ecotopes with names for the presently known ecotypes of the North Atlantic region. Based on Friend and Richardson (1986), Wildish (1988), Wildish (2017), Lowry and Myers (2019), and Myers (2022) with species names conforming to WoRMS (Horton et al. 2023), accessed in 2023.

Ecosystem	Primary Ecotope	Ecotype Name	Common Name	Example
Marine/Estuarine	Eulittoral wrack	Wrack generalist	Beach-hopper	*Orchestia mediterranea*
	Supralittoral wrack	Wrack generalist	Beach-hopper	*Orchestia gammarellus*
	Eulittoral salt marsh	Palustral	Salt-marsh-hopper	*Uhlorchestia uhleri*
	Supralittoral salt marsh	Palustral	Salt-marsh-hopper	*Speziorchestia grillus*
	Supralittoral mangrove	Mangal	Mangrove-hopper	*Chelorchestia forceps*
	Supralittoral sand-burrowing	Psammophile	Sand burrowing-hopper	*Americorchestia longicornis*
	Supralittoral driftwood	Xylophage	Driftwood-hopper	*Macarorchestia roffensis*
Freshwater	Plant drift-riverine	Riverine	Riverine-hopper	*Cryptorchestia cavimana*
	Plant drift-lacustrine	Lacustrine	Lacustrine-hopper	*Cryptorchestia garbinii*
	Non-tidal freshwater marsh	Freshwater palustral	Freshwater marsh-hopper	–
Terrestrial	Evergreen rainforest floor	Rain forest leaflitter	Leaf litter-hopper	*Palmorchestia epigaea*
	Soil- burrowing	Fossorial	Soil-hopper	–
	Marine caves	Troglobiont	Cave-hopper	*Palmorchestia hypogaea*
	Arboreal rainforest	Rain forest bryophile	Moss-hopper	–

Table 2. Primary ecotypes of marine/estuarine Talitridae. Comparing the coastal northwest Atlantic/Gulf of Mexico talitrids with those from the coastal northeast Atlantic/Mediterranean Sea. From Wildish and Chang (2017), all species names included below are given in Table 1 of this reference.

Primary ecotype	Numbers of Species		Number of shared species	Name of shared species
	NW Atlantic/ Gulf of Mexico	NE Atlantic/ Mediterranean		
Wrack Generalists	9	8	3	*O. gammarellus P. exter P. oliveirae*
Psammophiles	5	6	0	–
Palustrals	9	0	0	–
Xylophages	0	5	0	–
Troglobiont	0	1	0	–
Mangal	1	0	0	–

Table 3. Total body length (mm) of *P. exter* under various acclimation conditions (A to C). A Naturally acclimated to driftwood, collected in September 2014 and cultured for 6 months over winter in driftwood, from Wildish and Robinson (2016a). B Experimentally acclimated (~3 months) in culture with driftwood and collected from Haggerty's Beach in the summer of 2015. C Experimentally acclimated (~3 months) in culture with wrack (control) and collected from Indian Point in the summer of 2015. B and C from Wildish and Robinson (2016b).

Acclimation Conditions	Ecotope	Mean	Standard Deviation	N	Maximum	Minimum
A	Secondary	9.1	1.8	126	13.5	5.8
B	Secondary	11.5	1.7	32	15.9	6.3
C (Control)	Primary	12.7	1.8	42	16.6	6.3

In the control culture, treatment C of Table 3, total body length is significantly greater than in treatment A by t-test ($t = 11.225$, $df = 167$, $p < 0.001$), and C is also greater than B ($t = -2.952$, $df = 73$, $p < 0.005$). It was experimentally shown that slower growth rates were linked to lower standard metabolic rates (Wildish and Robinson 2018), suggesting that aged driftwood was more difficult to digest than aged macroalgal wrack. Experimental demonstration that *P. exter* can readily reverse the acclimation process from driftwood to wrack or vice versa has been obtained (Wildish and Robinson 2018). The mechanisms that produce dwarf morphs within *P. exter* because of a diet switch to driftwood remain unknown but could involve some form of phenotypic plasticity (see below).

Dwarf secondary ecotypic morphs have also been recognized in two other wrack generalists. The eulittoral wrack generalist *Orchestia mediterranea* A. Costa 1857 was found in a floating piece of driftwood that beached in the tidal Swale, Kent, England, containing 16 specimens (Wildish 2018 and references therein). The dwarf specimens of *O. mediterranea* were originally described as a new xylophagous specialist species, but the genetic data showed this was not the case (Wildish 2018). It is possible that *O. gammarellus* can also exist in a secondary driftwood ecotope (Wildish 2017). Thus, at least three species of secondary ecotype dwarf morphs associated with xylophagy have been identified and the primary ecotype of each is a wrack generalist, suggesting that this may be a general feature of this ecotype.

Orchestia gammarellus is also reported to live in European salt marshes (Sprung and Machado 2000; Dias and Sprung 2003; Schrama et al. 2015) rather than in the supralittoral drift line of beaches (primary ecotope), and this may be a further example of a secondary palustral ecotype. As far as I am aware, the morphological, physiological, and behavioral changes associated with a palustral ecotope for *O. gammarellus* have not been investigated. However, a change of diet from decaying macroalgae to decaying lignivorous salt marsh grasses is involved.

The generalist/specialist continuum

A generalist/specialist continuum within Talitridae was introduced by Wildish and Radulovici (2019) to help understand the ecological and evolutionary characteristics of this family. The generalist group of species are those capable of living in more than one ecotope and consuming a varied diet range. They contrast with specialist groups that live in a single ecotope and consume a singular diet.

Specific examples of primary ecotypes currently known from the North Atlantic coastal region are listed below in the same continuum order (generalist to specialist) shown in Table 4:

- # 1. Wrack generalists include *P. exter*, *P. oliveirae*, and *O. gammarellus*, which occur on both northeast and northwest Atlantic coasts. Wrack generalists limited to the northwest Atlantic coast are *Mexorchestia carpenteri carpenteri*, *M. c. radulovici-ae*, *Tethorchestia antillensis*, and *Platorchestia* sp. (identified genetically by Radulovici 2012). Limited to the northeast Atlantic coast are *Orchestia mediterranea*, *O. aestuarensis*, *O. montagui*, *O. xylino*, and *Speziorchestia stephensi.*
- # 2. Up to 7 genetically defined palustral species currently included within *Speziorchestia grillus* are confined to the northwest Atlantic coast.

- # 3. Different species of psammophilic talitrids occur on each side of the Atlantic: northwest: *Americorchestia longicornis*, *A. megalophthalma*, *A. heardi*, *A. salomani*, and *A. barbarae*; on the northeast: *Talitrus saltator*, *Deshayesorchestia deshayesii*, *Sardorchestia pelecaniformis*, *Britorchestia brito*, *B. ugolini*, and *Africorchestia spinifera.*
- # 4. Five species of xylophagous talitrids occur on the northeast Atlantic coast only: *Macarorchestia microphthalma*, *M. remyi*, *M. pavesiae*, *M. roffensis*, and *M. martini.*
- # 5. A single troglobiont in the northeastern Atlantic islands: *Palmorchestia hypogea.*

Of the five ecotopes in Table 4, the most variable one is the marine/estuarine supralittoral wrack zone. Wrack includes a wide range of different species of green, brown, and red macroalgae, driftwood (from natural tree fall and human discards), and may contain or be dominated by angiosperm leaf litter, including seagrasses such as *Zostera* sp. and *Posidonia* sp. Over the full range of a given wrack generalist species, for example, *O. gammarellus* from northern Africa to Norway, the composition of wrack is zoogeographically highly variable. In addition, each item of plant detritus in wrack may be at a different stage of the decay cycle. The amount of wrack at a given location varies temporally depending on tidal conditions (predictable) and wind effects (random and unpredictable). Thus, offshore winds may carry wrack and driftwood away as flotsam, while onshore winds may deposit new sources of wrack and driftwood. Because of the high degree of environmental variability, it is not surprising that species belonging to the wrack generalist ecotype are phenotypically plastic, e.g., in *P. exter* (as *P. platensis*, Stock 1996; LeCroy 2011), rendering morphological classification difficult.

Psammophilic talitrids (# 2 Table 4) are limited to sandy beaches into which they can make temporary burrows for residence during daylight hours. There are five species on the northwest Atlantic and six on the northeast Atlantic coasts. There is some evidence that psammophiles are selective feeders, choosing particular macroalgal species from wrack on which to feed. An example is *Talitrus saltator* in France, which prefers *Fucus serratus* over other wrack species (Adin and Riera 2003). At another location in Spain, *T. saltator* preferred two different species of brown (phaeophycete) seaweed wrack: *Sargassum muticum* and *Gongolaria baccata* (Olabarria et al. 2009). Such results suggest that availability (of a phaeophycete) within the local wrack determines the food choice. Most authors stress the importance of wrack aging (microbial decomposition) in food choice, thought to be because of increased nutritional value (Lastra et al. 2015) or the decomposition of grazer deterrent chemicals (phlorotannins) in brown macroalgae (Pennings et al. 2000).

Of the palustral ecotype (# 3 Table 4), there are possibly seven species on the northwest Atlantic coast, whereas in the northeast Atlantic, there are none. However, *O. gammarellus* may be present in salt marshes of the northeast Atlantic as a secondary palustral ecotype (see above, although experimental support that it is consuming seagrass leaf litter is lacking). Food available to salt marsh hoppers includes a range of salt marsh angiosperm plants, sometimes with the addition of marine macroalgae thrown into the marsh by storm winds or in flooding seawater. As far as I know, no studies on digestive physiology are available for talitrids where the primary ecotope is a salt marsh.

There are five known species of specialist xylophagous talitrids (# 4 Table 4) found only on the northeast Atlantic coast. They are obligate feeders on rotting driftwood. Recently, a new species of xylophagous talitrid was discovered in Thailand by Wongkamhaeng et al. (2022). It is the first driftwood hopper discovered outside the northeast Atlantic/Mediterranean region and is likely an example of convergent evolution.

The single species of cavernicolus talitrid (# 5 Table 4) occurs only in the northeastern Atlantic Islands, and its feeding habits have not been studied (as is true of all other troglobiontic talitrids so far discovered).

Table 4. Marine/estuarine talitrid ecotopes of the North Atlantic coastal region in continuum order. The most generalist is #1, and #5 is the most specialist. Note that #5 is technically a terrestrial taxon.

Biological Characteristic	Continuum order				
	1	**2**	**3**	**4**	**5**
Ecotype	Wrack generalist	Psammophile	Palustral	Xylophage	Troglobiont
Size: Total body length, mm	> 15	> 15	> 15, < 15	< 15	< 15
Ecotope Variability	Highest	→	→	→	Lowest
Passive Dispersal	Best	→	→	→	Worst
Reproductive Potential	Maximum	→	→	→	Minimum
Standard Metabolic rate	Highest	→	→	→	Lowest
Dorsal Epidermal Pigment Patterns	Present	→	→	→	Absent
Behavioural Activity pattern	Nocturnally active	→	→	→	Random activity
Predation Risk	High	→	→	→	Low
Random Escape Response	Most	→	→	→	Least

Microevolution in contemporary talitrids

Mechanisms of microevolution

A modern understanding of Neo-Darwinian evolution must consider both genetic and epigenetic mechanisms (Jablonka and Lamb 2014).

Speciation involving sexual or natural selection of genetic change may occur in the following ways:

- Allopatric, where some form of barrier divides a breeding population into two parts such that the barrier prevents interbreeding between the separated populations. Liu et al. (2018) studied psammophilic hoppers with molecular genetic methods and showed that populations separated by a land bridge evolved independently on either side of the bridge.
- Sympatric, where genetic change occurs within the same population and the genetic variants are naturally selected and evolve reproductive isolation mechanisms that prevent interbreeding with the parent population. Wrack generalists found on Gulf of Mexico shores, such as *Mexicorchestia carpenteri carpenteri* Wildish & LeCroy, 2014, and *Tethorchestia antillensis* Bousfield, 1984, may have evolved from a common ancestor in this way.
- Peripatric evolution occurs when an isolated peripheral population is formed on an oceanic island by immigrants from the continental mainland. On the island, they evolve to become reproductively isolated from the parent, producing a new sister species. An example is from the Azores archipelago, where the xylophagous *Marcarorchestia martini* Stock, 1989, evolved from a mainland ancestor of *Macarorchestia* sp., which arrived as an immigrant on the island of Terceira in a floating driftwood log (Stock 1989; Wildish 2017).
- Parapatric evolution occurs when a smaller population becomes partially isolated from the main population at the edge of its zoogeographic range, then becomes genetically differentiated and a new species. A possible example is *Orchestia aestuarensis* Wildish, 1987, which is limited in distribution to an isolated mesohaline section of lowland estuaries at the edge of the range of its sister (parent) species, *O. mediterranea* A. Costa, 1857 (but see below).

Microevolution involving epigenetically derived alternative phenotypes (polyphenism or polymorphism) occurs as a result of the following (West-Eberhard 1989, 2005):

- Allelic-switch, in which the alternative phenotype chosen by the individual depends on one or more alleles present on one or more switch genes.
- Combined allelic switch, in which the alternative phenotype is switched on or off by a combination of allelic and environmental stimuli.

The non-genetic cellular controls that switch genes on or off in epigenesis (epimutation) include DNA methylation, histone modification, and non-coding RNA action (Bossdorf et al. 2008). I know only one talitrid study of epigenetic variation (Baldanzi et al. 2017). It concerned the psammophilic talitrid, *Capeorchestia capensis* (Dana, 1853) and looked for differences in DNA methylation among geographically separate populations in South Africa, which were loosely linked to different temperature regimes.

Future work on epigenesis in Talitridae should be focused on wrack generalist hoppers (Table 4) because this ecotype experiences the most environmental variability. Some specific areas where epigenetic studies utilizing ecological genetic techniques might be fruitful are suggested in the following sections.

Biological interactions

Talitrids interact with many different species (intraspecific interactions are excluded) from viruses and bacteria to mammals and birds (Wildish 1988). All types of interspecific interaction can be found among talitrids, but here predation by other species is the only one considered. The chief predators of wrack generalists and psammophilic talitrids are birds, particularly many species of shorebirds that forage intertidally, such as seagulls, starlings, and crows, but less commonly mice and the blue fox (Wildish 1988). During dispersion wrack, generalists have also been found in the stomachs of inshore fish, indicating that they have been predated during passive dispersal at sea (Gibson and Robb 1996; Laffaille et al. 1999).

Wrack generalists and psammophiles remain hidden during the day, the former in and under wrack piles cast up by recent high tides and the latter in temporary supralittoral burrows made in the sand above the recent wrack so they remain in contact with moisture. Endogenous diel rhythms with maximum activity at night have been found in many species of wrack generalists and sand-burrowing hoppers (Wildish et al. 2021). In the latter study, xylophagous-acclimated *Platorchestia exter* Myers & Lowry (2023), living in a secondary ecotope (its primary ecotype is a wrack generalist), lost its endogenous diel rhythm. This finding could be of use in understanding control mechanisms in talitrid locomotory activity. The locomotor activity rhythm study of Wildish et al. (2021) was the first comparative study of talitrids that included most of the ecotopes of the North Atlantic. Thus, the marine eulittoral hyalid (proposed stem group of the talitrids according to Bousfield 1984) had a circatidal rhythm; the palustral *Speziorchestia grillus* Bosc, 1802; and the marine xylophagous *Macarorchestia remyi* (Schellenberg, 1950), both lacked an endogenous rhythm, and activity was random. These findings are consistent with the adaptive value of endogenous rhythms and diurnal cryptic behavior. This includes hiding in wrack or burrows during

daylight to avoid bird predators, which use vision to capture talitrid prey and are only active by day. An additional benefit of cryptic behavior during daylight is that talitrids avoid the high temperatures and desiccation caused by sunlight. The fact that permanently cryptic ecotypes, such as xylophagous and troglobiontic talitrids, have lost diel activity (Table 4), implies that the maintenance of this behavior is physiologically costly.

Foraging birds in the supralittoral attempt to capture wrack generalists and sand-burrowing hoppers, the former by disturbing the wrack and the latter by probing burrows. The typical response of wrack generalists to disturbance of their habitat is random jumping in all directions at once. This group response may confuse the predator and serve to limit the predator's success in capturing individual talitrids. The escape response is continued until each talitrid can find a hiding place that is both humid and dark. This is an area of talitrid research where future experimental studies might be focused on the behavioral interactions of predators and prey. The intensity and duration of the escape response decrease along the generalist-specialist continuum (Table 4). For palustral talitrids, the main predators are foraging fish (Vince et al. 1976). The presently known palustral talitrids associated with the northwestern Atlantic coastline are *Speziorchestia grillus* (Bosc, 1802), *Uhlorchestia uhleri* (Shoemaker, 1930), and *U. spartinophila* Bousfield & Heard, 1986 (although genetic evidence of Radulovici (2012) suggests that *S. grillus* could be divisible into up to seven new species). Kneib (1982) showed by field experiments that the zonation patterns, with *S. grillus* occupying the high marsh and *U. spartinophila* lower in the marsh, were controlled by tidal inundation patterns. This mirrors the findings of intertidal zonation patterns of talitrids, such as *Orchestia mediterranea* controlled by tidal levels on the northeastern Atlantic coast (Wildish 1988). Availability of palustral talitrids to the main fish predator, *Fundulus* sp., decreases at higher tidal levels, so that *U. spartinophila* was more vulnerable to predation than *S. grillus*. Nevertheless, *U. spartinophila* has one more behavioral adaptive strategy to avoid fish predation: it can climb the *Spartina* stems and hide in the axils (Covi and Kneib 1995). Little is known about the biotic interactions of both xylophagous and troglobiontic talitrids. Since the former spend most of the day in burrows and cracks in decaying wood and the latter spend their lives in caves (Table 4), they are unlikely to encounter bird or fish predators. Further study is needed to discover the nature of the biotic relationships they have with other invertebrates with which they share their habitat.

Another adaptive strategy to reduce predation on wrack generalists and sand-burrowing hoppers is for the talitrids to produce epidermal pigments, which are hypothesized (Wildish and LeCroy 2014) to provide camouflage as protection from visual bird predators. In *Mexorchestia* sp., the habitat backgrounds in Florida vary from white sand for populations living under digging pellets of fiddler crabs where wrack was absent to hiding within copious banks of wrack where the background was dark. This sets up selective pressure by bird predation in opposite directions depending on the type of background; thus, on white sand, selection favors a non-pigmented body pattern, whereas on a wrack background, a highly pigmented pattern is selected (Wildish and LeCroy 2014). The nature of the ultimate polyphenic control of dorsal pigment patterns is unknown. In general, the likelihood of finding epidermal pigment patterns decreases along the generalist-specialist continuum (Table 4), until in xylophagous and troglobiontic talitrids the epidermal pigments are absent.

Low salinity

Marine talitrids can penetrate estuaries and other bodies of water with reduced salinities, such as the Baltic Sea (Persson 2001). In an English lowland estuary, it was shown that two *Orchestia* spp. penetrating from the seawater end had very different salinity limits (Wildish 1970a, 1970b). Thus, *O. gammarellus* was found at salinities down to 5% of full-strength seawater, versus a lower limit of 52% for *O. mediterranea*. Beyond the saline limit for *O. mediterranea*, a second, closely related sibling species, *O. aestuarensis*, was found upstream of the salinity limit of *O. mediterranea* in the Medway estuary, where mesohaline salinities ranged from 31 to 52% of full-strength seawater (Wildish and Radulovici 2020). *Orchestia gammarellus* uses a different strategy for penetrating estuaries than *O. mediterranea.* Thus, eggs of *O. gammarellus* grown in vitro were killed at < 40% seawater, but if the eggs were allowed to mature in the living female marsupium (= brood pouch) at culture salinities down to 10%, they survived and successfully developed (Morritt and Stevenson 1993). The explanation for this result provided by Morritt and Spicer (1998) was that the female was able to control the osmotic concentration of the marsupial fluid so that development continued despite the lethality of ambient seawater to the eggs. By contrast, cultured adult females carrying young in the brood pouch of *O. mediterranea* in diluted seawater (42% full-strength seawater) increased the intermoult period, dropped more dead eggs, and caused selective female mortality (Wildish 1970a). All of these effects in dilute seawater resulted in reduced population fertility for *O. mediterranea.*

The response of *O. mediterranea* when confronted with dilute seawater < 52% seawater is to produce a polymorphic form with minor morphological differences (Table 5) and a better ability to tolerate dilute seawater (down to 31% seawater in the Medway estuary). The mechanism controlling the appearance of the mesohaline form is unknown, although Wildish and Radulovici (2020) have proposed two mechanisms to account for this involving either epigenesis or regular speciation. The first

Table 5. Biological comparisons of a sister species pair of *Orchestia*. Data from Wildish (1987) and Pavesi et al. (2014).

Biological Characteristic		Sibling Species Pair	
General	**Specific**	***O. mediterranea***	***O. aestuarensis***
Ecotope		Marine/ Estuarine	Estuarine only
Salinity	% Full-strength seawater	>52%	<52%
Morphology	Male P2 palm	Sinuous	Notched
	General spination	More	Less
	Female P2 basis	Anterior hump	No anterior hump
	Female P2 propodus	Larger	Smaller
	Dorsal pigment pattern	No mid-dorsal holes	2 mid-dorsal holes/segment
Genetics	Mitochondrial CO1 K2P	11%	
	Nuclear 18S K2P	0.33%	
	Nuclear 28S K2P	0.15%	

involves epigenesis, in which a polymorphic allele, or set of alleles, is carried within the euryhaline form and initiated by the low salinity conditions to produce the mesohaline form. After the initial epigenesis switch gene(s) are established, they become linked by genetic assimilation with an ability to breed at reduced salinity and the morphological changes shown in Table 5. The second alternative hypothesis is that the mesohaline form evolves by regular parapatric speciation.

The genetic findings (Pavesi et al. 2014) for the mitochondrial CO1 gene for all *Orchestia* populations studied suggest that the average K2P difference of 22% is two times greater than for the values between *O. mediterranea* and *O. aestuarensis* (Table 5). Coupled with the small genetic differences for nuclear genes, this suggests that *O. aestuarensis* recently diverged from *O. mediterranea.* Further experimental studies are needed to test the alternative low salinity switch hypotheses. It is considered that regular speciation mechanisms are an unlikely explanation to account for the appearance of *O. aestuarensis* in estuaries because the morphologies between estuaries are so similar (and this would not be the case if *O. aestuarensis* arose de novo in each estuary).

If the low salinity switch hypothesis proves to be supported, it would explain the geographical distribution conundrum of *O. aestuarensis*: how does it get to the isolated position in the mesohaline section of an estuary by passive dispersal? It is unlikely that it could be passively distributed from one estuary to another to reach the mesohaline part of the estuary. If the low salinity switch hypothesis is supported for *O. aestuarensis*, the answer is that the appropriate silent genes are carried there within the body of its sibling, *O. mediterranea*, utilizing the passive dispersal mechanisms of the latter. The low salinity then acts as a switch, turning on the genes for the mesohaline phenotype.

Dwarfness

Three talitrids have been shown to have natural populations living in a driftwood secondary ecotope: *P. exter* (Wildish and Robinson 2016a), *O. mediterranea* (Wildish et al. 2012), and *O. gammarellus* (Wildish 2017). All three can sometimes be found feeding on decaying driftwood, and this diet results in slower growth and dwarf morphology, although the only one where this has been experimentally verified is in *P. exter* (Wildish 2017).

Besides these wrack generalist taxa living in a secondary ecotope, there is one genus, *Macarorchestia* Stock, 1989, where driftwood is the primary ecotope. *Macarorchestia* currently has five specialist xylophagous species, which all appear to be obligate feeders on driftwood (Wildish 2017), although this has yet to be checked experimentally in three (*microphthalma*, *pavesiae*, *martini*) of the five *Macarorchestia* spps. Xylophagous specialist adaptations were reviewed in Wildish (2017) and include dwarfism, small eye size, females larger than males, and lack of dorsal pigment patterns. An experimental investigation of the ultimate causes of dwarfism in talitrids utilized *P. exter* acclimated to a driftwood diet (Wildish and Robinson 2016b). Two of the hypotheses: (1) dwarfism evolved to allow talitrids to live in and negotiate the small burrows made by gribbles (Isopoda, Limnoridae) after driftwood reaches the sea, and (2) driftwood was poor quality food, forcing reduced metabolism, growth, and adult maximum size, were both supported by the behavioral and physiological experiments undertaken. A powerful support for hypothesis (1) was that there is evidence that the *Macarorchestia* species form a series of declining sizes from *M. microphthalma* (largest) to *M. martini* (smallest) and that the serial dwarfism displayed by this xylophagous genus allows successively smaller species to occupy a greater percentage of gribble burrows because of their smaller size (Wildish and Robinson 2016b).

The underlying physiology of dwarfism in the xylophagous specialist genus *Macarorchestia* is contrary to the metabolic theory of Kingsolver and Huey (2008), according to which most Talitridae develop slower, mature slower, and achieve larger final body sizes the further they are from the equator (Wildish et al. 2011). Xylophagous populations reach smaller adult sizes not as a result of warmer temperature regimes but by adapting to living in ever smaller spaces.

Molecular genetic methods and talitrid microevolution

Modern molecular genetic methods utilize DNA markers, such as microsatellites, restriction fragment length polymorphisms, and DNA sequence data (Monsen-Collar and Dolcemascolo 2010). The development of polymerase chain reaction (PCR) methods has made it possible to use smaller amounts of genetic material in the analysis. The results of such studies could be used to determine:

- The amount of genetic variation within a population or species
- The degree of relatedness among populations/species (of use in taxonomy)
- Determine the evolutionary history of species and higher taxa (of use in evolutionary studies)
- If enough taxa are included, it can be used to construct phylogenies and estimate geological divergence times from a common ancestor.

To determine the amount of genetic variation within talitrid species, the earliest molecular genetic methods utilized allozyme electrophoresis. The results are summarized by Pavesi and Ketmaier (2013), and their review includes a list of 12 species each with an estimate of genetic diversity within each population sampled. The genetic structure of a population indicates the multiple factors affecting the genetic input it receives from immigrants arriving after dispersal and thus includes those that influence dispersal success between isolated 'island' populations (Wildish 2012). All of the wrack generalists included in Pavesi and Ketmaier (2013): *O. gammarellus*, *O. mediterranea*, *O. montagui*, and *P. exter* have low levels of genetic diversity, supporting the view that passive dispersal is high and/or that the distances between occupied ecotopes (or 'islands') are small. One anomalous species, *Speziorchestia stephensi*, is a wrack generalist but has a high level of genetic diversity. Apart from one riverine/lacustrine species, all the other talitrids were specialists (three psammophiles and one each of a xylophage, a troglobiont, and a rain forest leaflitter species) with a high level of genetic diversity. The results outlined by Pavesi and Ketmaier (2013) for wrack generalists, with the exception of *O. montagui* and *S. stephensi*, have a wider zoogeographic distribution outside the Mediterranean Sea along the northeast Atlantic coast. These results largely support the lineal 'island' theory of dispersal proposed by Wildish (2012).

With the mtDNA cytochrome oxidase I gene (CO1), Ketmaier et al. (2010) showed that in the psammophile *Talitrus saltator*, the degree of genetic diversity increased with decreasing shoreline erosion along the same beach. *Talitrus saltator* subpopulations had the least genetic diversity if the sandy beach sample location underwent irregular erosion events. Presumably this was because, at this location on the sandy beach, more talitrids were lost by storm events and received more fresh immigrants following storms and onshore winds. In another study using the CO1 gene and three Mediterranean populations of the xylophagous talitrid, *Macarorchestia remyi*, a deep split in genetic diversity between populations from the Adriatic and Tyrrhenian Seas was found (Pavesi et al. 2011). This is consistent with this xylophagous talitrid having low dispersal capability (Table 4). On further examination of individuals from both Adriatic and Tyrrhenian populations, small morphological differences were found, and a new species was described for the Tyrrhenian population (Wildish 2014).

Baldanzi et al. (2016) measured the genetic diversity with the CO1 gene of another psammophile, *Capeorchestia capensis*, distributed around the tip of South Africa. Eight locations were sampled along a coastal stretch of ~ 2500 km in a region where the Atlantic and Indian Oceans join. Like the Mediterranean sandhoppers described above, they also found deep genetic diversity, including three main haplogroups. Each of these was described as an evolutionary significant unit, loosely linked to the temperature regimes of the biogeographic provinces of South Africa. However, examination of the same populations of *C. capensis* by conventional morphological taxonomic methods (Lowry and Baldanzi 2016) found no differences between the three evolutionary significant units. Baldanzi et al. (2016) suggest that *C. capensis* at the southern tip of Africa has undergone cryptic speciation in forming a species complex. Subsequently, Baldanzi et al. (2017) found evidence in the same populations of indications of epigenetic variation among populations of *C. capensis* with the methylation-sensitive amplified polymorphism method.

Talitrid colonization of the North Atlantic Oceanic Islands

There are many islands present in the North Atlantic (International Hydrographic Organization 1953), of which only a few have been investigated to determine talitrid biodiversity. According to the influential model of island biogeography of MacArthur and Wilson (1967) and subsequent studies in insects (Peck and Finston 1993), the following factors might influence island occurrence by talitrids: island area, ecotope diversity on the island, the marine distance from the continental mainland, as well as island age. Factors affecting talitrid dispersal to oceanic islands include: emigration frequency from the donor population, the size of the donor population, and the dispersal capability of the transport raft (dependent on ocean current direction), including raft longevity (Wildish 2012).

As far as I am aware, only two oceanic islands have been studied sufficiently well to provide even a species list for the Talitridae occupying them. They are La Palma in the Canaries Archipelago in the eastern, and Bermuda in the western, North Atlantic.

La Palma in the Canaries Archipelago

The Canaries Archipelago is the closest of the northeast Atlantic islands to a continental land mass, with La Palma 445 km from North Africa. La Palma is semi-tropical (29°N) with a land area of 708 km^2, and although the Canaries is one of the older volcanic island chains in the northeast Atlantic at 20.5 MYA (Wildish 2012), La Palma was formed only 1.8 MYA. It has a diverse flora depending on altitude; thus, at 500–1400 m a laurel cloud forest is present. At lower altitudes from sea level upwards to 500 m are the endemic Canary Island pine forests. At altitudes greater than 1400 m, shrubs and heathland dominate (Aguilar et al. 2010).

Talitrid geographic distribution data for the islands of the Canaries Archipelago is spotty and almost certainly incomplete. Perhaps the best studied for talitrids is La Palma, due largely to the fieldwork of Jan Stock. Shown in Table 6 is the limited data available for the whole Archipelago.

The two *Talitroides* species are aliens, probably introduced synanthropically and limited to cultivated lands at lower altitudes. The three wrack generalists of Table 6 could be recent immigrants, arriving either by natural passive wrack rafting or by some form of synanthropy (Wildish 2012). The presence of a sandhopper on some of the Canary Islands suggests that *T. saltator* arrived relatively recently by synanthropy or was able to wrack raft from the mainland. The most interesting group is the five terrestrial leaf litter hoppers. The authors describing them suggested that they are individual island endemics, although much more comprehensive sampling is needed for all of the Canaries Archipelago islands before this claim can be substantiated. All five of the terrestrial species identified in Table 6 live in forest leaf litter, although their zoogeographic distribution on the islands of discovery remains unknown (apart from the two *Palmorchestia* spps). What is clear is that they are terrestrial species that evolved on the islands, where they are now found from marine ancestors that were naturally dispersed from the continental mainland.

Villacorta et al. (2008) present a field sampling and molecular genetic study of the two *Palmorchestia* species discovered by Stock and Martin (1988) and Stock (1990). Twelve localities were sampled throughout the island for a total of 89 individuals sequenced for the cytochrome oxidase mtDNA region (alignment length of 761 bp). Stock (1990) and Villacorta et al. (2008) both hypothesized that *Palmorchestia* originated from a supralittoral ancestor that migrated to a contiguous, ancient laurel forest leaf litter environment to become a terrestrial landhopper. During periods of drought on La Palma, the landhopper sought refuge in the lava tubes and caves that permeate the island and provide constant high humidity, where it became acclimated as a cavehopper. A more plausible alternative hypothesis is that the ancestor was a supralittoral driftwood hopper that arrived at a cave mouth opening in the supralittoral. The new immigrant first became acclimated to the cave environment before spreading throughout the island in the extensive lava tubes (Wildish 2012). *Palmorchestia* colonized a secondary ecotope, the contiguous humid laurel forest leaf litter at higher altitudes on La Palma. During periods of drought, leaf litter populations retreated to the cave environment, still carrying the dormant genes necessary for cave life. Wildish (2012) originally suggested a form of parapatric speciation to explain the driftwood ancestor hypothesis, but a more plausible explanation is that epigenetically derived alternative phenotypes within *Palmorchestia* populations occur on La Palma in response to the two contiguous ecotopes (hypogean and epigean). The driftwood hypothesis requires that *P. hypogaea* has an older origin than *P. epigaea* and that both are sister species and can partially interbreed. Inconclusive evidence in support of the driftwood ancestor hypothesis for *Palmorchestia* includes:

- Estimates of phylogenetic age suggest that *P. hypogaea* has an older common ancestor than *P. epigaea* (table 2 in Villacorta et al. 2008).
- The driftwood hypothesis does not require the laurel forest to be at sea level.
- The driftwood hypothesis does explain how *Palmorchestia* could reach both the northern and

Table 6. Talitrid fauna of islands in the Canary Archipelago, from Wildish (2012). Based on published systematic data to 1990. Generic names are corrected according to WoRMS (Horton et al. 2023) accessed in 2023.

Species names from WoRMS accessed 2023	Ecotype	Islands	Island Endemic
Insularorchestia monodi (Mateus, Mateus & Afonso,1986)	Wrack generalist	Many	No
Orchestia gammarellus (Pallas, 1766)	Wrack generalist	Many	No
Orchestia mediterranea A. Costa, 1857	Wrack generalist	Many	No
Talitrus saltator (Montagu, 1808)	Psammophile	Many	No
Cryptorchestia canariensis Dahl, 1950	Terrestrial	Gran Canaria	Yes
Canariorchestia gomeri Stock, 1989	Terrestrial	La Gomera	Yes
Speziorchestia guancha Stock & Boxshall, 1989	Terrestrial	Tenerife	Yes
Cryptorchesta stocki Ruffo, 1990	Terrestrial	Gran Canaria	Yes
Palmorchestia hypogaea Stock & Martin,1988.	Troglobiont	La Palma	Yes
Palmorchestia epigaea Stock, 1990	Terrestrial	La Palma	Yes
Talitroides topitotum (Burt, 1934)	Terrestrial	Many	No
Talitroides alluaudi (Chevreux, 1896)	Terrestrial	Many	No

southern ends of the island by active and passive dispersal within lava tubes.
- There is a precedent for a driftwood hopper, *Macarorchestia remyi*, being present in an Italian cave opening in the supralittoral of the island of Corsica (Schellenberg 1950).
- Both *Macarorchestia* and *Palmorchestia* species are small, with the ovigerous female larger than the adult male in both genera.

In a review of the troglobiontic insects of the Galapagos Islands, Peck and Finston (1993) describe many cases of eyeless cave and eyed epigean sister species (e.g., beetles), which are found in close but not overlapping geographic proximity. Peck and Finston (1993) hypothesize that the insect hypogean/epigean sister pairs arose by parapatric evolution, but it could involve epigenesis as explained above.

Bermuda

The volcanic eruptions that formed Bermuda first began some 110 MYA and ended some 30 MYA. The present-day Bermudian archipelago has a land surface area of only 53 km^2, and the nearest continental landmass is in North Carolina, U.S.A., some 1020 km distant (Wildish et al. 2016). Fluctuations in sea level during the Pleistocene led to extinctions of the terrestrial and littoral fauna, the last of which occurred at 0.4 MYA, when most of Bermuda was below sea level (Olson et al. 2006). Thus, faunal recolonization of Bermuda occurred relatively recently (< 0.4 MYA). A comprehensive survey of the supralittoral talitrid fauna (excluding palustral and most terrestrial ecotopes) revealed that only 5 talitrid species were present in 2014. The list shown in Table 7 excludes the one synanthropically introduced terrestrial, leaf-litter species. There are no endemics consistent with the short time (< 0.4 MYA) available for colonization and lack of ecotope variability on the island. Wrack generalists may reach Bermuda by natural rafting, but the picture is obscured because of synanthropic dispersal in modern times. Despite the availability of sandy beaches, no psammophilic talitrids were found on Bermuda (Wildish et al. 2016), consistent with their poorer dispersal ability (Table 4).

Macroevolution and the origin of the Talitridae

The following types of macroevolution might occur during a study of the phylogeny of talitrids:

- Divergence: a once interbreeding population splits into two or more species, and the new species becomes more dissimilar with time. Many of the wrack generalist talitrids may have originated by divergent evolution.
- Convergence: occurs when two species from different genetic backgrounds occupy the same or similar ecotope and, by adaptative processes, come to show the same phenotypic characteristics. An example is the troglobiontic talitrids, in which all species so far recognized have lost eyes and epidermal pigment patterns.
- Parallel evolution: occurs when two species from genetically different ancestor lines develop similar phenotypic traits when occupying the same ecotope. An example would be the behavioral escape response of jumping in random directions to confuse avian predators shown by co-occurring *Platorchestia oliveirae* and *Mexorchestia carpenteri carpenteri* in the Gulf of Mexico wrack (Wildish and LeCroy 2014).
- Coevolution: when two often radically different species influence each other's evolution to the benefit of both. An example is the wrack generalist *Orchestia montagui* feeding on wrack from *Posidonia* sp., which maintains a lignivorous bacterial species in the hepatopancreas capable of metabolizing the food that the talitrid eats (Abdelrhman et al. 2017). In return, the talitrid provides a suitable culture environment for the bacterium, which is rare or absent in the general environment.

A comprehensive fossil record for the Talitridae is absent. Currently, only three talitrid fossils have been discovered, two in Mexican amber (Bousfield and Poinar 1994; Hegna et al. 2020), the other from Dominican Republic amber (Bousfield and Poinar 1995), and all from 26–38 MYA. They were terrestrial species and are currently uninformative about their evolutionary history.

Table 7. Supralittoral talitrids of the Bermuda archipelago in 2014 (Wildish et al. 2016). BOLD = Barcode of Life Data System, available at www.boldsystems.org. WG = wrack generalist, T = terrestrial leaf litter hopper. 21 of 23 stations are occupied by talitrids.

Species names from WoRMS accessed 2024	BOLD	Ecotype	Number of stations occupied Total = 23	Percentage commonness
Platorchestia oliveirae Myers & Lowry, 2023	AAB3402	WG	12	52
Platorchestia exter Myers & Lowry, 2023	AAA2949	WG	4	17
Mexorchestia carpenteri carpenteri Wildish & LeCroy, 2014	AAC1491	WG	2	9
Tethorchestia antillensis Bousfield, 1984	–	WG	1	4
Talitroides alluaudi (Chevreux, 1896)	ACH9326	T	2	9

In classical taxonomy, a sufficient number of morphological characters must be chosen to distinguish between closely related populations and a subjective decision made by the taxonomist as to what constitutes a new species (Myers 1997). Such characters have also been used to infer the phylogeny of the Talitroidea. Thus, Bousfield (1982) used a phenetic analysis to do so within the Talitroidea, recognizing the problem of homoplasy and ecological overlap but apparently not correcting for them in his data matrix. More recently, Myers and Lowry (2020) have used a morphological cladistic analysis of the talitroids and determined for each character state whether the relationship was synapomorphic or homoplastic. A total of 46-character states were used in the analysis by Myers and Lowry (2020), of which 16 were zoogeographic in nature. Not surprisingly, there was little agreement between the two methods. A central problem with morphological reconstructions of amphipod phylogeny is that individual taxonomists use both a different number and quality of input data (morphological character states). Thus, in Bousefield's (1982) phenetic analysis, 60 character states were included, involving some overlap with those used by Myers and Lowry (2020). The quality of the input data in the latter study was clearly higher than in the former.

No equivalent molecular-genetic method has been attempted to determine the phylogeny of the Talitroidea. The input data for such a study would be drawn from the genetic material found in each eukaryote cell. This method does offer one advantage over the morphological ones discussed above: it can be used to estimate the time that elapsed when a common ancestor branched into two clades using the molecular clock approach (Ho and Duchêne 2014). Smaller-scale phylogenies of Lake Baikal amphipods (Macdonald et al. 2005), world-wide species of *Gammarus* (Hou et al. 2007), and Ponto-Caspian amphipods (Mamos et al. 2021) have been based on molecular genetic data. A first attempt at a phylogeny of the Amphipoda (including Talitroidea) using a dataset containing representative species from approximately one-half of the known families of Amphipoda was published by Copilaş-Ciocianu et al. (2019). Four common genetic markers (mitochondrial CO1, nuclear ribosomal RNA subunits 28S and 18S, and nuclear histone H3) were used, and divergence time estimates for the Talitroidea were 40–72 MYA, depending on which of three calibration methods were used. This preliminary result is supportive of the more recent origin (70–110 MYA) of the Talitridae suggested by Bousfield (1984).

Ideally, we would test a data set common between a morphological cladistic analysis and one where molecular genetic data was available from the same taxa. Unfortunately, no such study has been attempted, and we must conclude that both methods are still under development and that such a test is premature. Thought experiments suggest that for the morphological cladistic analysis it must yield results that are similar when performed by different taxonomists who may be using different numbers and quality of morphological character states. Similarly, for molecular genetic input data, we would expect the same results if different molecular geneticists ran the analysis and chose different types of input data (mitochondrial or nuclear genes). For both approaches, independent scientists producing similar results would be a good indicator that they had achieved a reproducible scientific method.

In the North Atlantic, apart from the three amphi-Atlantic talitrid species of Table 2, all remaining 41 species are not shared between the northwestern and northeastern Atlantic coastlines. This is interpreted as circumstantial evidence of vicariance, in this case, the formation of the North Atlantic Ocean by the spreading apart of tectonic plates (Bousfield 1984; Myers 2022), which separated the North American and Eurasian continents. Thereafter, when the last land bridge between North America and Eurasia was severed at ~ 50 MYA (Atlantic Geoscience Society 2001), the fauna, including talitrids, evolved independently on the two separated continents.

One common route of land colonization by Talitridae has been demonstrated using knowledge of geological events in the Pacific Ocean (e.g., temporal patterns of sea level rise) and molecular genetic methods (Yang et al. 2013; Liu et al. 2022). The mechanism involved marine supralittoral talitrids in East Asia, which were carried inland by marine incursions when global sea level was high at 10–17 MYA.

Discussion

Armed with the methods available to study ecology and microevolution, including field experimental ecological genetics (Ford 1975) coupled with modern molecular genetic methods and the new field of epigenetic evolution to explore, the student of these topics can make important discoveries with talitrids as the target. Both study areas are a good fit for young students of the Amphipoda keen to make fundamental discoveries with field biology methods. This is because so little has been achieved yet in either the ecology or evolution of the Talitridae. Another bonus for the aspiring talitrid student is that it will take you to interesting sampling locations.

We have seen in this review that the wrack generalist talitrids found in the Atlantic coastal region occupy an environment that offers the most variability: wrack, driftwood, salt marshes, and intertidal caves. Importantly, these are contemporary marine/estuarine ecotopes where each is adjacent or contiguous to each other and not solely dependent on passive dispersion to cross environmental boundaries. Passive mechanisms are thought to enable long-range dispersal (Wildish 2012). On the other hand, specialists occupy a single ecotope and have phenotypic adaptations specifically to it. The ecotopes of specialists become rarer as the continuum order becomes more specialized. Thus, caves that adjoin the marine intertidal are

uncommon and far apart, rendering passive dispersal to and from them virtually impossible. These results emphasize the primacy of the environment in shaping the talitrid species that exist today.

Whether all wrack generalists share the ability to respond to the different ecotopes available remains to be demonstrated with those species not yet studied ecologically. A pertinent question is whether specialist ecotypes share the phenotypical plasticity characteristic given the experimental or natural opportunity to do so. The *Palmorchestia* example studied by Villacorta et al. (2008) suggests that the specialist does retain phenotypical plasticity to respond to contiguous biotopes (cave to subtropical forest leaf litter) in response to an undetermined environmental switch. Specialist ecotypes generally experience less environmental variability than generalists.

An important realization from this review is that the initial stages of talitrid microevolution may be controlled by epigenetic mechanisms in response to specific environmental factors and aided by switch genes. Two of the best examples given above may qualify as involving epigenesis. The first is the sibling pair *O. mediterranea/O. aestuarensis*, where the environmental cue is low salinity (Wildish and Radulovici 2020), and the second is the hypogaean/epigean sibling pair of *Palmorchestia* spp., with the environmental switch undetermined. Sibling pairs of hypogaean/epigean species are found in many other invertebrates, such as insects (Peck and Finston 1993), and the existence of sister species pairs could be a general indicator that epigenetic mechanisms were involved in their formation. If epigenesis is involved in microevolution in the formation of cryptic species complexes (Baldanzi et al. 2016, 2017), it has implications for morphological systematics as currently practiced in the Talitridae (Myers and Lowry 2020, 2023). As we have seen, wrack generalist talitrids are biologically vagile, including in their morphology in responding to the ecotope variability that they meet throughout their zoogeographic range. Such a situation poses a problem for the biological species concept (Mayr 1942) and the morphological systematics of talitrids. Part of the solution involves the introduction of molecular genetic methods into the routine practice of systematics (Coleman and Radulovici 2020), as well as increased field sampling to discover new talitrids.

For variation in dorsal pigment patterns used as camouflage protection against avian predators, the genetic variation brought about by sexual reproduction, including crossing over during meiosis (Jablonka and Lamb 2014), may be key. Here, natural selection by bird predation at the population level can determine which pigment patterns survive against the background ecotope in which a population lives. For talitrid dwarfness, two environmental drivers have been identified. The first involves wrack generalists, such as *Platorchestia exter*, who, if they adopt driftwood as food, have a reduced standard metabolic rate, slower growth, and final body size, and if the usual wrack diet is offered, metabolism and growth rate are restored (Wildish and Robinson 2016a). The second case involves obligate driftwood-living talitrids of the genus *Macarorchestia*. The five species of this genus form a series of decreasing sizes, with the leading hypothesis being that they were adapting to gribble burrow hole diameters in driftwood (Wildish and Robinson 2016b).

Is it better to become a specialist or remain a generalist, that is, to specialize or not to specialize? The question is rhetorical and does not imply that the talitrid has a choice. The business end of the matter is the individual and population undergoing natural selection in response to the environmental limiting factors it has to face. The latter include those environmental limits involved in passive dispersal mechanisms of talitrids. Comparing the wrack generalist with the troglobiont (Table 4), the main difference between them is that there are many more individual locations available for the former than the latter. This results from the larger zoogeographic range of wrack generalists and therefore more nuanced ecotope variations to which it is exposed. The collateral effects that follow (Table 8) are that phenotypic variation is higher, the zoogeographic range is larger, speciation potential is lower, and endemism is lower in wrack generalists than in talitrid specialists. This implies the primacy of environmental variability in determining whether to speciate or not to speciate.

Table 8. Marine/estuarine ecotypes of the North Atlantic coastal region in continuum order and their evolutionary characteristics.

Evolutionary Characteristic	Continuum order				
	1	2	3	4	5
	Wrack generalist	Psammophile	Palustral	Xylophage	Troglobiont
Phenotypic Variability	Most	→	→	→	Least
Occurrence of Epigenetics	Most Likely	→	→	→	Least Likely
Zoogeographic Range	Greatest	→	→	→	Smallest
Speciation Potential	Low	→	→	→	High
Degree of Endemism	Lowest	→	→	→	Highest

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